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American Chestnut: Blight and the Resurrection of a Mighty Giant

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First…some history: A century ago, American chestnut was the largest and most abundant tree species in North America's eastern deciduous forests (Fig. 1), with typical mature specimens standing 75 – 100 feet tall and 24 – 48 inches in diameter. Pure stands of chestnut were common in the southern Appalachians and the species occupied 45 – 85% of overstory space throughout much of its 200 million acre range. In addition to sheer numbers, American chestnut was a crucial natural resource to the people of Appalachia and the forest industry in the eastern U.S. The straight-grained, decay resistant wood made excellent lumber for interior and exterior uses of all types from railroad ties and fence posts to furniture and fiddles. Furthermore, chestnut bark yielded prodigious amounts of tannin for treating leather, and the seasonal nut crops were both important food for woodland animals and much needed cash crops for rural communities. Over 400 million board feet of chestnut were harvested in the eastern U.S. in 1905 and in 1906, 45 million pounds of chestnut bark were processed for tannins. In West Virginia alone, the standing timber value of American chestnut in 1912 — the year the blight arrived in the state — was over $2 billion by today's monetary standards!

Fig. 1. (Left) Old-growth American chestnut in the Nantahala National Forest, North Carolina, ca. 1910 (courtesy of the The Forest History Society); (Right) A "chestnut family," Great Smokey Mountains, North Carolina ca. 1908 (courtesy of The American Chestnut Foundation).

What made chestnut such a successful competitor? First, chestnut just plain grew faster than other trees when it had sufficient light because a conspicuously high percentage of carbohydrates were directed to shoot growth at the expense of root growth. As long as moisture and nutrients were plentiful, the tree thrived. Chestnut was also moderately shade-tolerant permitting it to exploit low light conditions to get established until some overstory disturbance "released" it. Collectively, American chestnut utilizes a combination of life and growth strategies common to both early-successional (pioneering) shade-intolerant and late-successional shade tolerant tree species.

Tragedy Strikes

The chestnut blight fungus, *Cryphonectria parasitica,* is a canker pathogen capable of colonizing wounds created by self-pruning, winter injury, insects, woodland mammals, and mechanical injuries that expose the inner bark. The fungus likely was introduced into N. America from Japan in the late 1800s on infected nursery stock. The disease was first discovered in 1904 by H.W. Merkel, chief forester for the NY Zoological Park, on dying American chestnuts in the park. By 1912, the blight had spread as far north as the Hudson River Valley and Massachusetts, and as far south as northern Virginia and West Virginia. Within 50 years of the initial discovery, nearly 8.5 million acres of chestnut forests had fallen prey to the pathogen. The devastation incited by "the blight" was, and remains to this day, one of the greatest single transformative events ever recorded in a natural plant population. The nearly complete elimination of this ecologically important tree species significantly altered the structure, species composition, and successional patterns of eastern forests (Fig. 2). Albeit variable by region and elevation, no single species within the former oak-chestnut association has assumed the dominant and/or codominant role previously occupied by chestnut.

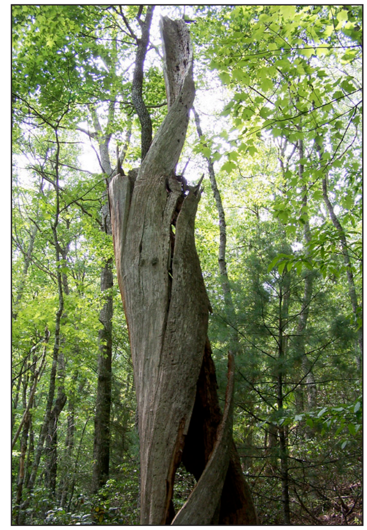

Fig. 2. "Old ghost," American chestnut snag, Jefferson National Forest, Virginia (S. Kenaley, 2008)

Despite this grim account, American chestnuts still grow throughout much of the original range. Contemporary populations are maintained primarily by the succession of sprouts from former seedlings and/or parent trees present before the arrival of the chestnut blight. Sprouts generally grow to heights of 6 – 12 feet and diameters of 1 – 2 inches before succumbing to the disease but some get to be twice that size. Upon the death of above ground shoots, a new generation of sprouts is released. Due to sparse nut production on young trees, this successive regeneration via sprouting likely saved the American chestnut from extinction.

Glimmers of Hope

By the early 1960s, American chestnut was thought to be doomed as all attempts to reduce the disease had failed to slow its inexorable progress. However, while American foresters wrung their hands in despair, stands of sweet chestnut (*Castanea sativa*) in Italy — devastated by nearly 25 years of chestnut blight — inexplicably were in recovery. Disease incidence remained high, but fewer trees were actually dying. This "recovery phenomenon" was confirmed by the French mycologist Jean Grente and later proven to be caused by a unique group of viruses — *Cryphonectria hypovirus*es — that reduce the virulence of the blight fungus. Grente's discovery prompted the deployment of virus-containing strains — otherwise known as hypovirulent ("less virulent") strains — in Europe as well as in N. America to attenuate the spread and intensification of chestnut blight. Presently, the natural spread of *Cryphonectria hypovirus 1*(*CHV1*), the most common virus in Europe, serves as an effective means of biological control in Italy, Switzerland, and France. However, over the last 30 years, efforts to artificially introduce and exploit *CHV1* as a biological control agent within the natural range of American chestnut were not so successful. The virus spread readily among cankers on individual trees; but tree-to-tree spread in forests has been limited. There is hope that improved deployment strategies and, more importantly, time may overcome current limitations permitting hypovirus-mediated biological control to be utilized as a single-treatment option or in concert with other restoration programs such as breeding or genetic engineering for blight resistance.

Breeding programs for blight resistance utilizing an interbreeding approach have been ongoing since 1930, but efforts to exploit resistance genes got a big boost in 1983 when American Chestnut Foundation (TACF) was founded with the explicit mission to fund Charles Burnham's proposed backcross breeding program (Fig. 3).

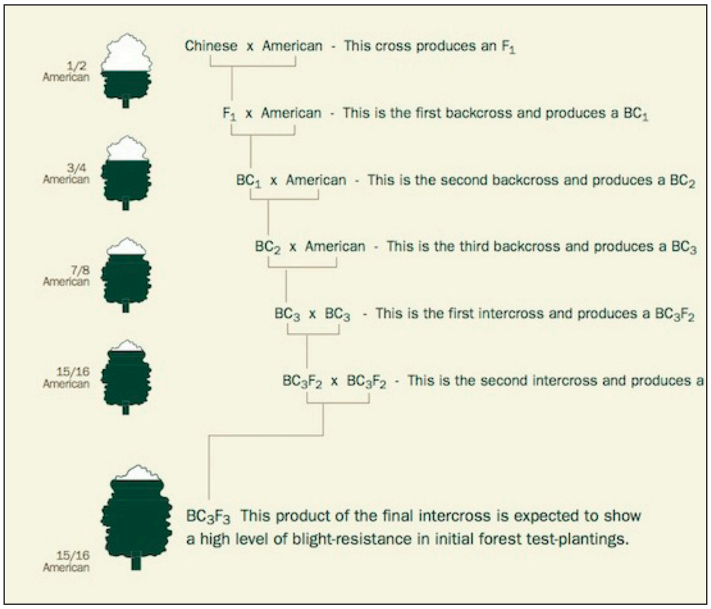

Fig. 3. Schematic of the backcross breeding program developed by Charles Burnham and presently executed by The American Chestnut Foundation.

Since its inception in 1989, the TACF program (method) has been under the direction of Dr. Fred Hebard and in its simplest form, the aim of this work has been to "create" an American chestnut genome with blight resistance genes from oriental chestnuts while preserving the desirable qualities of American chestnut (i.e., morphology and growth habitat). To do this, blight resistance genes are transferred from Chinese chestnuts (*Castanea mollissima*) to America chestnuts via simple hybridization. Progeny from the first cross — the first generation hybrids (F_1s) are genetically one-half Chinese and one-half American — are then crossed back separately to genetically different American chestnut resulting in backcross progeny BC_1F_1. Three successive rounds of backcrossing concomitant with selection for blight resistance and against Chinese traits that are not intimately linked to resistance progressively decreases the proportion of Chinese chestnut genes by a factor of one-half per cross while yielding third backcross trees (BC_3F_1s) that look and grow like American chestnut. Because blight resistance is partially (incomplete) dominant, BC_3F_1s with different parentage are then intercrossed to produce BC_3F_2 trees fully segregating for resistance (Fig. 4). Moreover, multiple cultivars of Chinese chestnut and first backcross trees — such as the 'Clapper' and 'Graves' trees — have been introduced into the breeding lines as resistance sources. Presently, the TACF program has achieved blight-resistant BC_3F_3 trees that will ultimately be grown in nut orchards for continued breeding and, as Dr. Burnham likely envisioned over 30 years ago, nut for forest introduction trials!

With recent advances in molecular biotechnology, the opportunity to restore American chestnut via genetic modification is also within grasp. Transformation research in chestnut has evolved rapidly over the last decade, focusing on the development of traditional

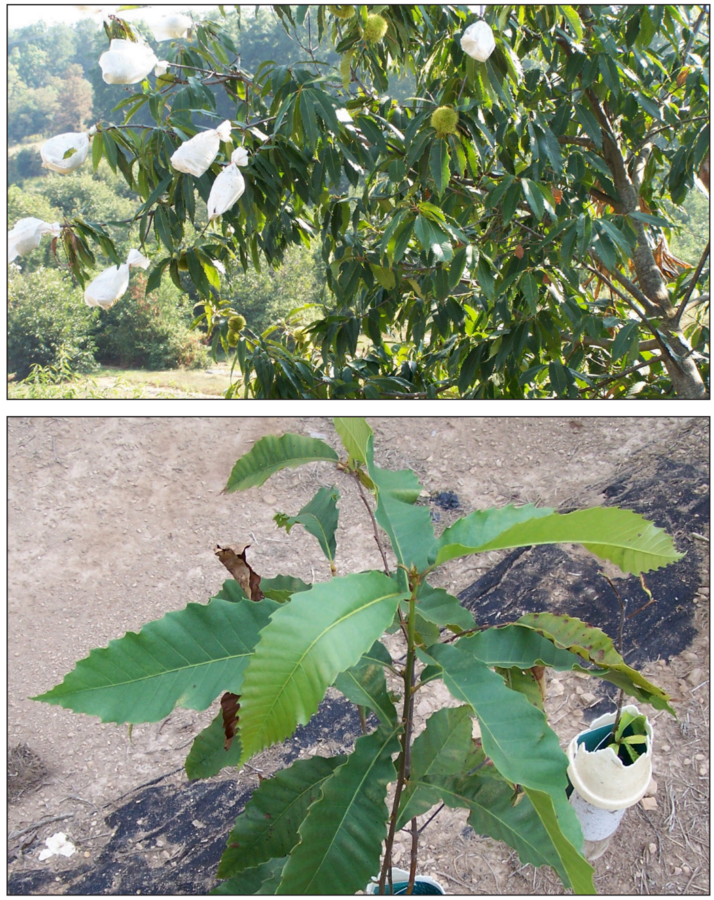

Fig. 4. (Top) Controlled pollination, backcrossing (Bottom) and third-generation backcross hybrid American chestnut (S. Kenaley, Meadowview, VA, 2007).

transgenic methods to introduce pest resistance genes found in model pathosytems — such as the oxalate oxidase gene found in wheat — into chestnut as a means to counteract the chemical arsenal employed by the chestnut blight fungus. However, a novel approach called cisgenics is also in development. Unlike transgenics, cisgenic tree improvement harnesses the ever-increasing power of genomic sequencing and bioinformatics to locate and map blight resistance genes in Chinese as well as Chinese x American chestnut families. Candidate resistant genes will then be cloned separately, or in combination, and inserted into the genome of pure American chestnut. Resultant trees would, in essence, be equivalent to backcross chestnuts relative to blight resistance, yet, their genomes would be over 99% of American origin, and the time of production from transformation to a flowering tree would be three years. Regardless of the approach, the creation of resistant chestnuts through genetic engineering will provide a promising foundation for restoration efforts.

Much work is left to be done to ensure that previous efforts associated with the development of blight-resistant chestnuts are fully realized. Moreover, because forests once home to American chestnut have undergone considerable change over the last century, the implications of these changes on future restoration efforts remain uncertain. Likewise, because American chestnut previously was the dominant tree species in many sites, and its reintroduction now or anytime soon may also have potential, and unforeseen, influences on native plant and animal populations that have adapted to thrive it the absence of chestnut. Nonetheless, we are now on the brink of an exciting new phase in the restoration of American chestnut that will perhaps end in the largest reforestation the country has ever seen. There *is* hope.